

THE MAMMALS OF CATANDUANES ISLAND: IMPLICATIONS FOR THE BIOGEOGRAPHY OF SMALL LAND-BRIDGE ISLANDS IN THE PHILIPPINES

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Abstract.—Thirty-five species of mammals are known from Catanduanes Island, 28 of which are reported here for the first time; these include 1 insectivore, 24 bats, 1 primate, 5 rodents, 2 carnivores, and 2 ungulates. No endemic species are present, and all but one (the widespread *Saccolaimus saccolaimus*) are known from neighboring Luzon. All populations are morphologically similar to conspecifics on Luzon. Data are consistent with the prediction (based on depth of surrounding water) that Catanduanes should exhibit characteristics associated with being a small land-bridge island of the Luzon faunal region. The avifauna of Catanduanes shows similar biogeographic patterns.

Although the mammalian fauna of Luzon Island is considered to be one of the best-known in the Philippine Archipelago, none of the small islands offshore of Luzon had been comprehensively surveyed at the time of the last faunal review (Heaney 1986, Heaney et al. 1987). This is unfortunate, since knowledge of the faunas of small islands often provides the basis for inferences about the dynamics of evolution and extinction within island archipelagos (Case & Cody 1983, Heaney & Patterson 1986), and such studies within the Mindanao and Palawan regions of the Philippines have been productive (Heaney 1986, Heaney et al. 1989). Accordingly, the small islands surrounding Luzon (which has a rich fauna of endemic murid rodents and pteropodid bats) may be expected to be especially interesting for studies of evolutionary biogeography.

This paper reports the results of a survey of the mammals of Catanduanes Island, an island that lies adjacent to the southern peninsula of Luzon. Published records previously existed for only seven species of mammals (Heaney 1986). Because little has been published on the ecology of most species of small mammals in the Philippines, we include here data on reproduction and descriptions of habitats where the animals were taken. Geographic variation in most Phil-

ippines species is poorly documented, so we have provided external and cranial measurements wherever possible. We use these data to test several predictions of biogeographic patterns proposed earlier (Heaney 1986, Heaney et al. 1989).

Climate and Geology of Catanduanes

Catanduanes is an island of 1513 km² that lies 8 km east of the nearest portion of the southeastern peninsula of Luzon. Because the highest point is 764 m, the island is below the elevation required to support more than small and localized areas of montane or mossy vegetation (Heaney et al. 1989, Whitmore 1984). In about 1970, primary forest was estimated to cover about 25% of the island, with about half of the remaining area covered by secondary forest (observations by PCG). By 1988, the Philippine Bureau of Forest Development estimated that primary forest occupied about 5% of the island, with about 25% of the island covered by scattered patches of degraded primary and second-growth forest.

Catanduanes lies in one of the principal typhoon tracks in eastern Asia, and rainfall is thus both high and seasonal. Mean annual rainfall at Baras, Pandan, and Virac is 5481,

3149, and 2971 mm, respectively; there is no month of the year at any of these sites that receives less than 100 mm (Manalo 1956). Although our 1988 sampling period occurred during one of the drier times of the year, it rained nearly every day. For additional description of the island and a treatment of its avifauna, see Gonzales (1983) and Goodman & Gonzales (1989).

Catanduanes is a part of the Eastern Philippine Rim Structural Region, and lies just to the west of the northern portion of the Philippine Trench, where the Pacific Plate is actively subducted below the Philippines. Volcanic activity associated with this subduction has produced 1966 m (Mt. Isarog) and 2462 m (Mt. Mayon) basaltic/andesitic cones on southern Luzon, about 60 km to the west and southwest of Catanduanes. Although there are no volcanic products on Catanduanes, the island is subject to frequent earthquakes; we experienced one registered at 6.9 on the Richter scale during our 1988 season. Most of the island is composed of Cretaceous to Eocene shales and limestone that have been partially metamorphosed into schist and marble; some soft coal of the same age is present. The southern tip of the island is composed of Recent to Pleistocene corals, reef limestones, beach deposits, and marine sediments; these limestones contained the caves that we investigated. The present island mass was upraised during Pliocene to Recent times, in association with the tectonic activities that caused the development of the region's prominent volcanic cones (Hamilton 1979, Hashimoto 1981, Philippine Bureau of Mines 1963).

Current water depth separating Catanduanes from Luzon is about 50 m. It is therefore virtually certain that Catanduanes was a part of the island of Greater Luzon during the late Pleistocene (i.e., from about 25,000 to about 10,000 years ago), when sea level was about 120 m lower than at present (Heaney 1986).

Methods

Field studies were conducted during two periods. The first phase extended intermittently from May 1968 to June 1971; specimens were collected at four forest sites by PCG and a team from the Philippine National Museum in conjunction with studies of the avifauna of Catanduanes (Gonzales 1983). The second period of intensive mammal investigation extended from 12 to 28 February 1988; specimens were collected at two forest sites and two caves by a joint team from the United States National Museum of Natural History (USNM; Washington, D.C.), the Philippine National Museum (PNM; Manila), and Silliman University (SU; Dumaguete). Sampling during phase two followed methods used on Leyte, Negros and other islands in 1987 (Heaney et al. 1989) in order to facilitate comparisons.

During phase two, bats were caught in mist nets set on ridgetops, across trails and streams, at the edges of clearings adjacent to forest, and inside caves. Nets were tended continuously during the primary activity peak from early dusk (about 17:30) until about 21:00, and some were tended longer; nets were left open thereafter, and bats were removed at dawn. We also captured several *Miniopterus* spp. in Cave 1 in a butterfly net, and one *Hipposideros obscurus* from a hollow log in a fragment of a mist net. During the first phase, nets were examined in late afternoon and at dawn, and occasionally during the evening.

Non-volant small mammals were caught in traps; during the first phase all traps were Victor rat snap-traps (ca. 75%) and National live traps (ca. 25%). Phase two traps were baited late each afternoon with fresh fried coconut coated with peanut butter, and checked each morning soon after dawn; they were checked occasionally in the early afternoon and evening as well. Traps were placed 5 to 15 m apart; most (95%) were

placed on the ground, but ca. 5% were placed above ground on fallen trees, horizontal branches, large vines, etc. Trap lines were run for three to five days, usually four. Phase one traps were baited daily, and were handled in a fashion similar to that for phase two, but in a less standardized manner.

Temperatures during 1988 were recorded daily with minimum-maximum thermometers that were maintained in shaded spots about 1.5 m above the forest floor. Tree diameter at breast height (DBH) was estimated so as to exclude buttresses.

Voucher specimens were prepared in fluid, as skeletons, or as skins with partial skeletons, and have been deposited at the USNM and the PNM. In 1988, specimens were autopsied in the field for reproductive information. Size of embryos was measured as crown to rump length (CRL). Subadult animals are defined here as those that have not completed cranial growth, especially those having unfused basicranial sutures. Comments on distribution and use of scientific names are based on Heaney et al. (1987) unless stated otherwise. Records of specimens examined are summarized at the end of each account whenever this is not obvious within the account; such summaries include site number and number of specimens (in parentheses).

Comparison of fruit bat species richness and netting success from phase two sampling with data from other islands was standardized to exclude *Pteropus leucopterus* because we are often unable to sample the large flying foxes (*Acerodon* and *Pteropus*) that forage at the top of the forest canopy, and so have not included these species in other analyses (Heaney et al. 1989).

External measurements and weights reported here were taken by the authors in the field on fresh animals in 1988. All cranial measurements were taken by LRH with digital calipers graduated to 0.01 mm. Comparisons of cranial measurements are to published records of specimens also mea-

sured by LRH. Some comparisons were made with specimens in the University of Michigan, Museum of Zoology (UMMZ).

Study Sites

We surveyed mammals at six forest sites (four in 1969–1971 and two in 1988) and two caves sites (both in 1988); these are referred to in the species accounts by number. Additional minor sites are described in the species accounts.

Site 1 (2 days in May 1968).—Located in the municipality of Dugui-too, north of Virac at 300–400 m elevation in mixed primary forest, second growth, and recently logged areas.

Site 2 (2 days in June 1969).—Located in Barrio San Pedro, in Gigmoto Municipality, at 200–300 m in moderately to very steep terrain, in patchy primary forest, second growth with abundant *Musa* sp., and cultivated land along the Gigmoto River.

Site 3 (2 days in June 1969).—Located in Matamok Barrio in Caramoran Municipality, east of Caramoran at the top of a small promontory (ca. 200 m) in moderately steep terrain, in a mixture of low primary forest and second growth with patches of abaca (*Musa textilis*).

Site 4 (2 days in June 1971).—Located in Barrio Balinad in Viga Municipality, east of Viga in low rolling hills along the Balinad River (100–200 m) in patchy primary forest, second growth, and agricultural clearings.

Site 5 (8 days in 1988).—Located 8½ km W of Gigmoto at 250 m elevation (13°47'N, 124°19'E) in primary forest on a small plateau between two rivers. Ground slope was slight, rarely exceeding 20°. Temperatures ranged from nighttime lows of 20.5° to 23.5°C to daytime highs of 23.5° to 26.0°C, with daily temperature ranges of 1.5° to 4.5°C. The tallest trees (mostly dipterocarps, including *Shorea* sp.) in the sampling area were about 25 m and had large but-

tresses; the canopy was 15–20 m but was discontinuous because many of the trees with the largest diameters (DBH 1.0 to 1.3) were broken off at 20 to 25 m, giving the impression that the frequent typhoons often seriously damage the forest. Epiphytic vines, ferns, and orchids were common on upper branches of large trees; moss was present but rare. Scattered slender palms (*Livistona*) reached the canopy; we noted no fig (*Ficus*) trees. The broken canopy allowed much light to penetrate to the forest floor, and vegetation near the ground was heavy, with saplings, small ground palms, sapling *Livistona* palms, broad-leaved herbaceous plants, viny rattan, and many viny pandans (*Freycinetia* sp.) commonly represented, as well as a few scattered erect terrestrial pandans (*Pandanus* sp.) and wild bananas (*Musa* sp.). Fallen trees and portions of trees were common; leaf litter was light. A small clearing (ca. 1 ha) was located within our study site; no traps were set in the clearing, but 14 net-nights were from nets set at the edge.

Site 6 (7 days in 1988).—Located 8½ km W, 1 km N Gigmoto at 200 m elevation (13°48'N, 124°19'E) along the dirt road from Summit to Gigmoto that briefly parallels then crosses the Buadan River, within about 0.75 km of human habitation sites. The river was a clear, fast-moving stream, 5–10 m wide and up to 1 m deep in a rocky bed 10–20 m wide. The area was one of low hills, with banks along the river 20 to 40 m high and often steep (up to 60°, typically 45°). The forest was similar to that at Site 2, but logging and clearing for agriculture had left a mosaic of primary and secondary forest, second growth, and active fields. Tree height was similar, but the protected slopes along the river supported more unbroken large trees (up to 35 m), including figs (*Ficus*). Abaca (*Musa textilis*), wild banana (*Musa* sp.) and tree ferns (*Cyathea* sp.) were common in secondary forest and old fields. Traps and nets were set in all habitats.

Cave 1.—Luyan Cave, located 3 km E, ¾ km N of San Andres at an elevation of 80 m (13°36'N, 124°8'E), is along the main road

from Virac to San Andres. The cave is in a region of rugged limestone ridges that occupies much of southern Catanduanes. Nearby vegetation was about half agricultural land and half heavily disturbed secondary forest, with forest predominating on the steep slopes near the cave. The entrance to the cave is a recreational area and a religious shrine, with concrete steps and flooring within the well-lit entrance area. The cave was about 300 m long, with entrances at both ends, and with a small side-passage; there was abundant evidence of flooding. The main passage was 8–10 (up to 15) m wide and usually 15 m high (up to 20 m). It was heavily disturbed by guano miners and bat hunters; the bats were skittish. The ceiling and walls were rather smooth, with some solution holes and stalactites.

Cave 2.—A small cave, located 4 km W of Virac in the barrio of Pajo at an elevation of 50 m (13°35'N, 124°11'E), is on a hillside adjacent to the Pajo River in a large limestone outcropping. Nearby vegetation was predominantly agricultural land (mostly rice fields), but heavily disturbed secondary forest occurred along the steep hillsides. The main entrance was small (2 m high × 1.5 m wide) and partly shrouded by bushes and bamboo. The cave was rather short (about 30 m long), with vertical height of 2–4 (rarely up to 5) m and width of 2–3 (rarely to 4) m. A second entrance lay at the opposite end of the cave; this entrance was small (0.5 × 0.5 m) and partly blocked by vegetation and rubble. Two side passages were present, one 5 m long and 4 m wide, and the other about 8 m long and rather narrow (2 m high and 1.5 m wide). The ceiling and wall surfaces were irregular, with numerous stalactites and cracks, and rough, crumbling surfaces.

Accounts of Species

Order Insectivora—Insectivores

Family Soricidae—Shrews

Crocidura grayi.—This poorly-known species has been reported previously only

from Luzon and Mindoro (Heaney et al. 1987). A single specimen (with a badly damaged skull) was found dead in 1988 on the road from Summit to Gigmoto, about 4 km E of Summit by road (250 m elevation) in an area of mixed degraded secondary forest and agricultural land.

Order Chiroptera—Bats

Family Pteropodidae—Fruit Bats

Cynopterus brachyotis.—A common, widespread species in Southeast Asia. Most common in disturbed habitat, but present in primary forest (Table 4). In February 1988, nine adult females were multiparous with large nipples but were not lactating; all were pregnant with single embryos (CRL = 3, 5, 7, 8, 10, 14, 15, 18 mm). Four subadults with unfused phalangeal epiphyses had small nipples; two were not pregnant, and two had single embryos of 4 and 5 mm. Five adult males had testes of 3×2.5 , 4×5 , 5×3 , 5×4 , and 7×4 ; a subadult had testes of 1×1.5 mm. Crania are larger than those from Negros and Camiguin, but are nearly identical to a series from Quezon Province (Table 1; Heaney 1984; specimens in UMMZ). Records: Site 1 (2); Site 2 (6); Site 4 (1); Site 5 (5); Site 6 (33).

Eonycteris robusta.—One specimen of this uncommon, poorly known Philippine endemic was captured at Site 2, and two primigravid females were captured at Site 6 on 22 and 24 Feb. 1988; each carried a single embryo (CRL = 3 and 8 mm). Cranial measurements (Table 1) of these specimens fit well within the range of specimens from Luzon and Negros (Heaney & Rabor 1982; specimens in USNM).

Eonycteris spelaea.—A widespread species in Southeast Asia, common in disturbed habitats. One was captured at Site 2 in 1969, and two adult females from Site 6 were pregnant with single embryos of 9 and 12 mm CRL on 22 and 25 February 1988. Cranial measurements (Table 1) are similar to those from Luzon and Negros (Heaney & Rabor 1982; specimens in USNM).

Haplonycteris fischeri.—A Philippine endemic; we found them to be most common in primary forest (Site 5), but present in disturbed forest (Site 6), as is typically the case (Heideman & Heaney 1989). We frequently heard them produce chittering calls in the canopy in the evening at Site 5. In late February 1988, four adult females had large nipples but were not lactating; each carried a single embryo of 3 or 4 mm CRL. Two subadult females had small nipples, and each carried a single embryo of 2 mm CRL. Three adult males had testes 3×3 , 3×3 , and 4×4 mm. Cranial measurements (Table 1) are similar to those of a series from Luzon, and are slightly larger than those from Dinagat and Negros (Heaney & Rabor 1982; specimens in USNM). Records: Site 4 (5); Site 5 (14); Site 6 (5).

Macroglossus minimus.—A common, widespread species in Southeast Asia. We found them to be most abundant in disturbed habitat (Site 6; Table 1); at both Site 5 and 6 they were taken in or near clumps of wild banana and/or abaca, as is often the case (Heideman and Heaney 1989). In February 1988, two adult females were not pregnant, and six each carried a single embryo of 3, 4, 4, 10, 16, and 22 mm CRL; two were both pregnant and lactating. A single primigravid subadult female had small nipples and a single embryo (CRL = 1 mm). Eight adult males had testes of 6×4 to 8×7 mm, and six subadults had testes of 1×1 to 5×3 . Cranial measurements (Table 1) are very similar to a series from Negros, but bats from both islands are slightly larger than those from Camiguin and Mindanao (Heaney 1984; specimens in USNM). Records: Site 1 (1); Site 2 (2); Site 5 (1); Site 6 (35).

Ptenochirus jagori.—A common Philippine endemic; in 1988 we found them only at the disturbed forest site (Site 6; Table 1), where they were abundant. Two adult females had large nipples but were not lactating; both carried single embryos of 3 and 4 mm CRL. Two subadult females had small nipples; one was nulliparous, and the other

Table 1.—Means ($\pm$ SD) and ranges of selected measurements of adult fruit bats (Pteropodidae) from Catanduanes Island, Philippines.

Species	Sex	n	Condylobasal length	Zygomatic width	Mastoid width
<i>Cynopterus brachyotis</i>	m	5	27.60 $\pm$ 0.49 (27.3–28.3)	18.72 $\pm$ 0.55 (18.3–19.6)	11.84 $\pm$ 0.22 (11.6–12.0)
<i>Cynopterus brachyotis</i>	f	4	28.23 $\pm$ 0.62 (27.6–28.9)	18.85 $\pm$ 0.48 (18.4–19.4)	11.95 $\pm$ 0.25 (11.7–12.3)
<i>Eonycteris robusta</i>	f	2	32.55 (32.3–32.8)	19.45 (19.3–19.6)	13.90 (13.8–14.0)
<i>Eonycteris spelaea</i>	f	2	33.10 (32.6–33.6)	19.95 (19.8–20.1)	13.35 (13.3–13.4)
<i>Haplonycteris fischeri</i>	m	5	24.16 $\pm$ 0.76 (23.2–25.2)	16.42 $\pm$ 0.13 (16.2–16.5)	10.70 $\pm$ 0.19 (10.4–10.9)
<i>Haplonycteris fischeri</i>	f	5	23.90 $\pm$ 0.37 (23.4–24.4)	16.04 $\pm$ 0.50 (15.4–16.7)	10.48 $\pm$ 0.51 (9.7–11.1)
<i>Macroglossus minimus</i>	m	6	25.23 $\pm$ 0.47 (24.4–25.7)	14.78 $\pm$ 0.59 (13.7–15.3)	10.05 $\pm$ 0.10 (9.9–10.2)
<i>Macroglossus minimus</i>	f	4	25.03 $\pm$ 0.46 (24.4–25.5)	13.63 $\pm$ 0.42 (13.3–14.1)	9.83 $\pm$ 0.19 (9.7–10.1)
<i>Ptenochirus jagori</i>	m	5	34.08 $\pm$ 0.69 (33.1–34.6)	24.34 $\pm$ 0.91 (22.8–25.1)	14.28 $\pm$ 0.22 (14.0–14.6)
<i>Ptenochirus jagori</i>	f	3	33.73 $\pm$ 0.40 (33.5–34.2)	23.50 $\pm$ 0.79 (22.6–24.1)	14.2 $\pm$ 0.0 (14.2)
<i>Pteropus leucopterus</i>	m	1	58.1	33.3	20.5
<i>Rousettus amplexicaudatus</i>	f	1	34.9	20.9	13.9

carried a single embryo of 7 mm CRL. Adult males had testes of 5 $\times$ 4 to 7 $\times$ 5, and subadults of 2 $\times$ 2 and 3 $\times$ 2. Cranial measurements (Table 1) are similar to those from central Luzon, and are smaller than those from Camiguin and Negros; adults possess the slightly paler, duller pelage of specimens from Luzon, rather than the darker pelage of those from Negros (Heaney & Rabor 1982, Heaney 1984; specimens in USNM). Records: Site 1 (2); Site 2 (7); Site 4 (2); Site 6 (19).

Pteropus leucopterus.—A rarely captured flying fox endemic to the Philippines, previously known only from Dinagat and Luzon. Two subadult males were netted on a high, denuded ridge at Site 6; both had small testes. Cranial measurements (Table 1) fall

within the range reported by Heaney & Rabor (1982).

Pteropus vampyrus.—This widespread Southeast Asian species was reported from Virac by Thomas (1898). Local hunters reported the presence of large flying foxes that could have been this species or *Acerodon jubatus*, or both; they were said to be diminishing in numbers and to be hunted actively.

Rousettus amplexicaudatus.—We captured a single specimen of this common, widespread Southeast Asian species at Site 6; it was a non-pregnant subadult female. A large colony of fruit bats observed but not captured in Cave 1 was probably composed of this species, although they may have been *Eonycteris spelaea*. Cranial measurements

Table 1.—Extended.

Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
11.50 ± 0.26 (11.2–11.9)	9.46 ± 0.31 (9.1–9.9)	6.72 ± 0.32 (6.3–7.2)	6.18 ± 0.44 (5.7–6.9)	14.10 ± 0.33 (13.6–14.5)	62.4 ± 3.8 (57–66)
11.93 ± 0.36 (11.6–12.4)	9.45 ± 0.21 (9.2–9.7)	6.60 ± 0.08 (6.5–6.7)	6.45 ± 0.35 (6.1–6.8)	14.13 ± 0.55 (13.3–14.4)	65.5 ± 0.6 (56–66)
12.0 (12.0–12.0)	12.35 (12.2–12.5)	8.95 (8.9–9.0)	7.75 (7.6–7.9)	18.00 (17.8–18.2)	73.5 (73–74)
12.15 (11.7–12.6)	11.20 (10.8–11.6)	8.10 (8.1)	7.5 (7.5)	18.05 (17.9–18.2)	71.0 (70–72)
10.22 ± 0.57 (9.6–11.1)	8.56 ± 0.36 (8.1–8.9)	5.90 ± 0.26 (5.6–6.2)	5.06 ± 0.32 (4.6–5.4)	11.62 ± 0.31 (11.3–12.1)	51.0 ± 1.4 (49–52)
9.82 ± 0.43 (9.3–10.4)	8.18 ± 0.22 (8.0–8.5)	5.72 ± 0.19 (5.4–5.9)	5.06 ± 0.40 (4.5–5.6)	11.70 ± 0.37 (11.1–12.0)	50.4 ± 1.5 (48–52)
8.23 ± 0.41 (7.8–8.9)	9.02 ± 0.35 (8.7–9.5)	5.42 ± 0.18 (5.1–5.6)	5.25 ± 0.18 (5.0–5.5)	13.52 ± 0.45 (12.7–13.9)	42.3 ± 1.0 (41–44)
7.90 ± 0.20 (7.8–8.2)	8.73 ± 0.21 (8.5–8.9)	5.50 ± 0.22 (5.3–5.8)	5.10 ± 0.18 (4.9–5.3)	13.63 ± 0.25 (13.3–13.9)	42.8 ± 1.0 (42–44)
15.28 ± 0.68 (14.4–16.0)	12.04 ± 0.21 (11.8–12.3)	8.54 ± 0.25 (8.2–8.9)	7.78 ± 0.43 (7.3–8.4)	17.38 ± 0.35 (16.9–17.8)	82.4 ± 1.7 (80–84)
15.13 ± 0.21 (14.9–15.3)	11.80 ± 0.30 (11.5–12.1)	8.27 ± 0.23 (8.0–8.4)	7.40 ± 0.26 (7.2–7.7)	17.00 ± 0.17 (16.8–17.1)	80.3 ± 0.3 (77–83)
22.0	22.1	16.2	12.4	31.2	134
13.3	13.8	10.7	8.6	18.3	82

fall within the range of series from Luzon, Mindanao, and Negros (Heaney & Rabor 1982, specimens in USNM).

Family Emballonuridae—Sheath-tailed Bats

Emballonura alecto.—We captured a single adult male of this species, which is known from throughout the Philippines, Borneo, and Sulawesi. It was netted in a darkened portion of Cave 1; others were seen high on the walls in moderately-lit portions. Cranial measurements (Table 2) are similar to those from series from Camiguin and Guimaras (Heaney & Rabor 1982, Heaney 1984).

Saccolaimus saccolaimus.—Two specimens were reported from Pandan, Catanduanes by Hollister (1913), and named as

a new species (*Taphonycteris capito*). Lawrence (1939) synonymized this taxon with *Taphozous* (*Saccolaimus*) *pluto* Miller (1910; from Mindanao), since both fell within the range of variation of a series from Mindoro. Goodwin (1979) and Koopman (1984) have shown *Saccolaimus saccolaimus* to be a widespread and variable species, and Philippine populations to fall within the range of variation for the species as a whole (specimens in USNM). Lawrence (1939) incorrectly stated that Pandan is in southern Luzon; her error was based on a change in the extent of Albay Province, which included Catanduanes in 1913 but did not in 1939. Cranial measurements (Table 2) fall within the range of specimens from Negros (specimens in USNM).

Table 2.—Means ($\pm$ SD) and ranges of selected measurements of adult insectivorous bats from Catanduanes Island, Philippines.

Species	Sex	n	Condylolincisive length	Zygomatic width	Mastoid width
<i>Emballonura alecto</i>	m	1	13.6	8.5	7.6
<i>Saccolaimus saccolaimus</i>	f	1	22.9	16.0	13.7
<i>Megaderma spasma</i>	m	1	23.1	14.6	11.6
<i>Megaderma spasma</i>	f	1	23.5	14.9	11.5
<i>Hipposideros ater</i>	m	5	14.10 $\pm$ 0.19 (13.9–14.1)	7.78 $\pm$ 0.05 (7.7–7.8)	8.32 $\pm$ 0.11 (8.2–8.4)
<i>Hipposideros ater</i>	f	3	14.50 $\pm$ 0.40 (14.1–14.9)	7.83 $\pm$ 0.12 (7.7–7.9)	8.40 $\pm$ 0.0 (8.4)
<i>Hipposideros diadema</i>	m	3	26.57 $\pm$ 0.32 (26.2–26.8)	16.33 $\pm$ 0.55 (15.7–16.7)	13.90 $\pm$ 0.26 (13.7–14.2)
<i>Hipposideros obscurus</i>	m	1	17.2	10.9	10.1
<i>Hipposideros obscurus</i>	f	1	16.5	10.8	9.5
<i>Rhinolophus arcuatus-s</i>	m	1	18.7	9.6	9.5
<i>Rhinolophus arcuatus-l</i>	m	1	19.5	9.9	10.0
<i>Rhinolophus inops</i>	m	2	21.85 (21.7–22.0)	10.9 (10.9)	10.7 (10.6–10.8)
<i>Rhinolophus inops</i>	f	2	21.65 (21.6–21.7)	10.9 (10.9)	10.4 (10.3–10.5)
<i>Rhinolophus rufus</i>	m	1	28.6	14.6	13.2
<i>Rhinolophus virgo</i>	m	1	15.5	8.5	8.1
<i>Miniopterus australis</i>	m	5	12.80 $\pm$ 0.22 (12.5–13.1)	7.30 $\pm$ 0.23 (6.9–7.5)	7.36 $\pm$ 0.11 (7.2–7.5)
<i>Miniopterus australis</i>	f	5	12.70 $\pm$ 0.16 (12.5–12.9)	7.32 $\pm$ 0.08 (7.2–7.4)	7.32 $\pm$ 0.15 (7.1–7.5)
<i>Miniopterus schreibersii</i>	m	3	15.03 $\pm$ 0.21 (14.8–15.2)	8.47 $\pm$ 0.16 (8.4–8.6)	8.47 $\pm$ 0.15 (8.3–8.6)
<i>Miniopterus schreibersii</i>	f	3	14.66 $\pm$ 0.21 (14.5–14.9)	8.33 $\pm$ 0.06 (8.3–8.4)	8.17 $\pm$ 0.15 (8.0–8.3)
<i>Murina cyclotis</i>	m	1	16.6	10.8	8.9
<i>Scotophilus kuhlii</i>	f	2	17.85 (17.7–18.0)	13.45 (13.0–13.9)	11.75 (11.6–11.9)

Family Megadermatidae—False Vampire Bats

Megaderma spasma.—A widespread species in Southeast Asia. One adult male was netted above a steep slope along the road at Site 6; additionally, one specimen (adult female, 1 embryo, CRL = 11 mm) was netted and several others seen in the main passage of Cave 2. The specimens are slightly larger than two from Mindanao (Heaney & Rabor 1982).

Family Rhinolophidae—Horseshoe-nosed Bats

Hipposideros ater.—A widespread species in Indo-Australia. Thirty to forty individuals were sighted and eleven captured at Cave 2. A few individuals were seen in dimly-lit portions of the main passage, but most were at the end of an entirely dark, narrow side passage. Three adult females were pregnant with single embryos (CRL = 7, 7, 8 mm). The crania are virtually iden-

Table 2.—Extended.

Orbital length	Canine to last molar	Molariform tooththrow	Palatal breadth	Palatal length	Forearm length
5.8	5.4	4.1	3.0	5.0	45
9.2	9.6	6.9	6.3	7.0	71.3
7.8	9.0	6.9	3.9	7.2	59
7.8	9.1	7.2	3.7	7.2	63
4.94 ± 0.09 (4.9–5.1)	4.86 ± 0.05 (4.8–4.9)	3.96 ± 0.15 (3.8–4.2)	3.22 ± 0.15 (3.0–3.4)	4.98 ± 0.15 (4.8–5.2)	40.8 ± 0.4 (40–41)
5.00 ± 0.10 (4.9–5.1)	4.93 ± 0.15 (4.8–5.1)	3.97 ± 0.06 (3.9–4.0)	3.23 ± 0.06 (3.2–3.3)	5.10 ± 0.10 (5.0–5.2)	42.0 ± 1.0 (41–43)
9.73 ± 0.45 (9.3–10.2)	10.67 ± 0.15 (10.5–10.8)	8.23 ± 0.30 (7.9–8.5)	7.17 ± 0.15 (7.0–7.3)	10.47 ± 0.31 (10.2–10.8)	—
6.9	6.6	5.7	5.2	6.2	48
6.5	6.5	5.1	5.2	6.2	47
5.4	7.5	5.5	4.0	6.3	45
5.6	8.0	5.9	3.9	6.5	47
6.25 (6.2–6.3)	8.85 (8.8–8.9)	6.45 (6.4–6.5)	4.50 (4.5)	7.65 (7.5–7.8)	51.0 (49–53)
6.10 (6.0–6.2)	8.90 (8.8–9.0)	6.60 (6.6)	4.70 (4.6–4.8)	7.55 (7.4–7.7)	50.5 (50–51)
7.9	11.9	8.9	6.5	10.7	68
4.8	6.2	4.6	3.6	5.6	43
4.22 ± 0.22 (3.9–4.5)	5.08 ± 0.08 (5.0–5.2)	3.70 ± 0.10 (3.6–3.8)	2.94 ± 0.05 (2.9–3.0)	5.94 ± 0.32 (5.5–6.2)	36.0 ± 0.7 (35–37)
4.12 ± 0.13 (3.9–4.2)	5.12 ± 0.08 (5.0–5.2)	3.70 ± 0.0 (3.7)	2.84 ± 0.09 (2.7–2.9)	5.52 ± 0.08 (5.4–5.6)	36.2 ± 0.4 (36–37)
5.30 ± 0.17 (5.2–5.5)	6.23 ± 0.06 (6.2–6.3)	4.47 ± 0.06 (4.4–4.5)	3.53 ± 0.06 (3.5–3.6)	6.70 ± 0.26 (6.4–6.9)	44.7 ± 0.6 (44–45)
5.13 ± 0.12 (5.0–5.2)	6.07 ± 0.12 (6.0–6.2)	4.33 ± 0.06 (4.3–4.4)	3.43 ± 0.06 (3.4–3.5)	6.47 ± 0.21 (6.3–6.7)	43.5 (43–44)
6.0	6.0	4.9	3.7	7.7	—
7.0 (7.0)	6.80 (6.8)	5.40 (5.4)	5.00 (4.8–5.2)	7.85 (7.7–8.0)	50.2 (49.0–52.0)

tical to a series from Luzon (specimens in USNM).

Hipposideros diadema. — A common species, widespread in Indo-Australia. Three specimens in the USNM from Baras and Pandan were reported by Hollister (1913); we captured none.

Hipposideros obscurus. — A poorly-known Philippine endemic species previously known only from Dinagat, Luzon, and Mindanao. We captured two individuals at Site 5, an adult female (not pregnant) in a mist

net on a low ridge in primary forest and an adult male that we saw roosting at the closed end of a hollow in a log less than 50 m from the netting site. The log was ca. 10 m long and from 1.0 to 1.6 m in diameter, and the hollow 6 m long and 0.4 to 0.6 m in diameter; dim light penetrated to the roosting site. Cranial measurements are slightly larger than those of one specimen from Dinagat (Heaney & Rabor 1982) and identical to a series from Luzon (in USNM).

Rhinolophus arcuatus. — Studies current-

ly in progress indicate that two very similar species that are present in the Philippines have been reported under this name: a slightly smaller species (designated "*R. arcuatus-s*" in Table 2) that is associated with lowland caves and a slightly larger species ("*R. arcuatus-l*") that is associated with upland primary forest. J. E. Hill (in litt.) has suggested that these are *R. arcuatus* and *R. anderseni*, but we have not examined the holotype of *R. anderseni* in Madrid, and so identification remains uncertain. We captured an adult male of the larger species in a ridge-top clearing at Site 6, and an adult male of the smaller species in Cave 1 in a very dimly-lit portion of the main passage. Cranial measurements (Table 2) for each are typical of larger series from Negros (specimens in USNM).

Rhinolophus inops. — A poorly known Philippine endemic, previously reported only from Luzon, Mindanao, Mindoro, and Negros (Heaney et al. 1987; specimens in USNM). We captured six and saw many more in the main passage of Cave 1. One adult female was pregnant with a single embryo (CRL = 3 mm); the other was not pregnant. Four adult males had testes of 1×1 or 1×2 . Cranial measurements (Table 2) fall within the range of those from Luzon and Negros (specimens in USNM).

Rhinolophus rufus. — A single specimen of this poorly known Philippine endemic was captured and several others seen in 1988 in a shallow rock overhang along a small river that is about 8 km W Gigmoto.

Rhinolophus virgo. — An endemic species widespread within the Philippines. We netted a single adult male on a low ridge in primary forest at Site 5.

Family Vespertilionidae—Common Bats

Miniopterus australis. — Both this and the following species are widespread in Indo-Australia. We netted 32 *M. australis* and 7 *M. schreibersii* from a colony of several hundred *Miniopterus* in a very dim portion of the main passage of Cave 1; many were

roosting in small groups (from one to five) inside small solution holes in the ceiling. All females were adults; all had tiny uteri and none were lactating. The adult males had tiny testes.

Miniopterus schreibersii. — In addition to the seven netted at Cave 1, we captured one *M. schreibersii* along the road above the river at Site 6. Three adult females had tiny uteri and were not lactating; five adult males had testes of 1×1 mm or less.

Murina cyclotis. — Widespread in Southern Asia; known previously in the Philippines from single specimens from Luzon and Mindanao (Heaney et al. 1987). We netted one adult male along the edge of the road above a steep drop to the river at Site 5.

Scotophilus kuhlii. — Three specimens in the USNM of this common, widespread commensal species from Pandan were reported by Hollister (1913); we captured none, but saw several bats flying over Virac that probably were this species.

Order Primates

Family Cercopithecidae—Monkeys

Macaca fascicularis. — PCG saw monkeys on a number of occasions in 1968–1971 at localities scattered around Catanduanes, and considered them to be moderately common. In 1988, hunters reported their presence to us, but said that they had declined and were absent from many parts of the island. No specimens are available.

Order Rodentia

Family Muridae—Rats and Mice

Apomys microdon. — A very poorly known species (Musser 1982), recently taken on Mt. Isarog in southern Luzon (Rickart et al. 1991). The single specimen, the holotype of the species, is from Biga (=Viga; Hollister 1913); we captured none. No information on the habitat or mode of acquisition of this specimen is on file at the USNM.

Phloeomys cumingi. — A very poorly known species previously reported only from southern Luzon and Marinduque. This giant arboreal rat was said by local hunters and farmers to be fairly common in 1988, and they obtained 13 specimens for us. These were captured in a hilly area that is a mosaic of degraded forest on steep slopes and agricultural land on less steep slopes; much of the cleared land consists of old, heavily vegetated patches of abaca and coconut and scattered tall trees. All were found by dogs in hollow logs or live hollow trees; they were driven out with smoke and fire and captured either by the dogs or by hand. Several of the standing trees were described as slanted; all were at least 40 cm in diameter.

Local hunters and farmers reported these animals to be strictly nocturnal and principally arboreal, always to nest in hollow trees, to have one young at a time and typically one young per year, and usually to live singly or in pairs (mother and offspring or adult male and female) although larger groupings had been seen. They were said to feed on tender young leaves of trees (especially red, flushing leaves), not to damage crops, and to be hunted occasionally for their meat.

Of two adult males obtained in February 1988, neither (1.74 and 1.95 kg) appeared to be in breeding condition; testes of one were 15×10 mm. One young adult male (1.45 kg) had testes 8×5 mm. Two nulliparous subadult females weighed 1.14 and 1.15 kg. Adult females ($n = 6$) ranged in weight from 1.45 to 2.1 kg; two had single nursing young that weighed 480 and 665 g, and each had a single discernable uterine scar. Four adult females had no uterine scars and were not lactating. These data indicate that births take place during the late rainy season (roughly December). The lack of reproductive activity in middle to late February (other than lactation) suggests that there is a lull in breeding activity at least during the dry season (late January to May,

and perhaps early rainy season (June to August) as well.

Cranial measurements (Table 3) are slightly smaller than those of a series from Mt. Isarog, southern Luzon, and much smaller than those of *P. pallidus* from central and northern Luzon (specimens in USNM). Pelage of all specimens was entirely dark brown, as is typical for this species, rather than the pale gray and dark brown of *P. pallidus*.

Rattus everetti. — We trapped this common but ecologically poorly-known Philippine endemic at Site 3 in 1969, and at Sites 5 and 6 in 1988. Most individuals at Site 5 were trapped adjacent to or beneath logs or at the base of trees, nearly always where there was cover from the logs or leafy vegetation. At Site 6, we caught these rats in both remnant forest and in heavily disturbed agricultural areas. At both sites animals were caught most often in steep areas, and rarely on flat ground except where there were fallen logs. One released rat initially hid on the ground in a tangle of vines and dead leaves; when chased it ran quickly and easily up the trunk of a large tree. One animal was caught during daylight hours, and all others at dusk or after dark.

Three subadult males with abdominal testes taken in February 1988 weighed 190–230 g; testes were 12×6 mm or smaller. Males with scrotal testes ($n = 17$) weighed 230–420 g; testis size ranged from 19×11 mm to 45×17 mm. Nulliparous females ($n = 15$) weighed from 110 to 270 g. No females with embryos were captured. Females with placental scars weighed 245–350 g; three apparently primigravid females (245, 260, 285 g) had 3, 5, and 10 scars, respectively. Multiparous females ($n = 8$) weighed 280 g or more, and retained several sets of uterine scars so that counts were not possible (one showed at least 18 scars). Records: Site 3 (7); Site 5 (45); Site 6 (8).

Rattus exulans. — Hollister (1913) described *Rattus leucophaetus* (now considered a synonym of *Rattus exulans*; Musser

Table 3.—Means ($\pm$ SD) and ranges of selected measurements of adult murid rodents from Catanduanes Island, Philippines. Values in brackets were taken by LRH on dried skins.

Species	Sex	n	Condylobasal lenth	Zygomatic width	Mastoid width	Rostral length
<i>Apomys microdon</i>	?	1	—	—	—	—
<i>Phloemys cumingi</i>	m	2	77.68 (75.3–80.0)	40.30 (39.3–41.3)	23.55 (23.5–26.5)	32.90 (31.6–34.2)
<i>Phloemys cumingi</i>	f	3	75.27 $\pm$ 3.72 (27.2–79.4)	40.23 $\pm$ 1.36 (38.8–41.5)	22.73 $\pm$ 0.92 (22.2–23.8)	32.23 $\pm$ 1.56 (30.8–33.9)
<i>Rattus everetti</i>	m	9	50.39 $\pm$ 2.99 (47.0–57.1)	25.53 $\pm$ 1.44 (23.5–28.1)	18.58 $\pm$ 0.30 (18.2–19.1)	20.50 $\pm$ 1.41 (18.7–23.3)
<i>Rattus everetti</i>	f	7	48.87 $\pm$ 2.22 (45.9–52.0)	24.15 $\pm$ 0.79 (23.4–25.1)	17.75 $\pm$ 0.64 (17.0–18.6)	20.06 $\pm$ 1.14 (18.3–21.7)
<i>Rattus exulans</i>	f	1	27.3	14.3	12.3	10.0

1977) on the basis of a single specimen from Bagamanoc, Catanduanes. We trapped a single specimen of this widespread commensal species in scrubby second-growth forest along the riverbank at Site 6.

Rattus rattus.—Hollister (1913) reported three specimens of this abundant commensal from Bagamanoc, Catanduanes; the USNM also contains specimens from Baras (1), Calolbon (2), Caramoran (1), Gigmoto (1), Pandan (2), and Viga (1). Six specimens were trapped at Site 3 in the same trap lines where 7 *R. everetti* were taken. We trapped a single adult male in primary forest at Site 5, in a trap under a small log at the base of a large tree; the same trap later captured a *Rattus everetti*.

Order Carnivora
Family Viverridae—Civets

Paradoxurus hermaphroditus and *Viverra zangalunga*.—PCG saw a captive *Viverra zangalunga* near Site 2 in 1969. He also saw an animal at dusk, near Kangkoyawe in 1968, that he believed to be *Paradoxurus hermaphroditus*. In 1988, local hunters and farmers from the vicinity of Site 6 described these two species of small carnivores to us, giving sufficient details that we are confident of their identities. Both were said to be moderately common. No specimens are available.

Order Artiodactyla
Family Suidae—Pigs

Sus barbatus.—PCG heard numerous reports of successful pig hunts from 1968 to 1971, and saw tracks and areas where pigs had rooted in the forest floor. In 1988, hunters and farmers reported the presence of wild pigs, but said that they were heavily hunted and restricted generally to a few inaccessible areas of the island. No specimens are available.

Family Cervidae—Deer

Cervus mariannus.—PCG saw an adult male Philippine brown deer that had been shot near Dugui-too in 1968, and heard of other successful hunts in other areas. In 1988, hunters and farmers reported deer to be nearly extinct on the island; no one we talked with knew of any being captured in the last few years. No specimens are available.

Results and Discussion

To summarize the critical points of the description of Catanduanes given above: (1) there was a land-bridge connection to Luzon in the recent past; (2) the island is rather small in total area; and (3) the vegetation was originally predominantly lowland dipterocarp forest. These points and the dis-

Table 3.—Extended.

Orbital length	Molariform toothrow	Palatal breadth	Diastema length	Head & body length	Tail length
	5.4	5.5	6.6	[103]	[136]
25.00	17.25	16.75	22.70	385.5	—
(24.5–25.5)	(17.2–17.3)	(16.3–17.2)	(22.4–23.0)	(370–401)	—
24.60 ± 0.85	17.90 ± 0.70	16.40 ± 0.17	21.43 ± 1.01	352.3 ± 30.4	327.0 ± 4.2
(23.7–25.4)	(17.1–18.4)	(16.2–16.5)	(20.8–22.6)	(330–387)	(324–330)
18.43 ± 0.79	9.23 ± 0.41	9.37 ± 0.23	14.37 ± 1.21	239.2 ± 12.9	244.3 ± 9.4
(17.4–20.0)	(8.7–9.8)	(9.1–9.7)	(13.0–17.0)	(222–260)	(234–257)
17.96 ± 0.63	9.31 ± 0.30	9.30 ± 0.43	14.00 ± 0.82	225.0 ± 15.5	229.4 ± 7.0
(17.1–18.4)	(8.9–9.7)	(8.5–9.8)	(12.7–15.1)	(203–242)	(222–242)
10.3	5.1	5.9	6.9	[118]	[108]

cussion and predictions in Heaney (1986), Heaney et al. (1989), and Heaney (1991) led us to predict (before visiting the island in 1988) that the island should be characterized by 1) a mammalian fauna shared entirely with Luzon, 2) species richness lower than that of Luzon, with species richness of non-volant mammals falling on or near the species richness/area curve for the Mindanao faunal region, 3) the species richness of fruit bats falling on the species richness/area curve for other fruit bat faunas in the Philippines, and 4) a fauna composed of species found at low to moderate elevations on Luzon.

Adequacy of sampling.—Before considering the data collected, it is important to consider the likelihood that current information reflects the total mammalian species richness of Catanduanes. We believe that there are five principal habitats that need to be sampled on any given Philippine island in order to assess the fauna: lowland forest, montane forest, mossy forest, second growth, and caves (Heaney et al. 1989, Rickart et al. 1991). We judge current trapping and netting samples from lowland forest to be minimally acceptable. Recent studies in the Philippines have shown that our 1988 samples of 100 fruit bats from primary forest and forest/clearing mosaic locality are likely to approximate species richness and proportional abundance, although rare spe-

cies may be missed (Heideman & Heaney 1989). Similarly, trapping samples based on 900 traps-nights are adequate to document species richness and rough proportional abundance, but again rare species may be missed (Heaney et al. 1989, Rickart et al. 1991). In both cases, important prior records supplement these lists. Thus, our lowland forest samples probably include most fruit bats and small non-volant mammals that are present, but a few gaps may remain.

No reliable estimates of Philippine microchiropteran faunas are available, and so no comparisons are possible. However, with 15 species recorded, Catanduanes has one of the richer known faunas.

Our samples from caves and second growth are less extensive, and are unlikely to be complete; more sampling is needed.

Most importantly, we were unable to sample either montane or mossy forest. Although Catanduanes has a maximum elevation of 764 m, which is below the lower limits of montane and mossy forest on large mountains (1000 m and 1500 m, respectively; Heaney et al. 1989, Rickart et al. 1991), we have found montane forest as low as 650 m and mossy forest as low as 900 m on Leyte (Heaney et al. 1989), and believe both may be present on Catanduanes as isolated fragments. Although bats tend to be rare in both habitats, at least one species (*Harpyionycteris whiteheadi*) occurs pri-

Table 4. —Numbers of fruit bats (Pteropodidae) captured in mist nets in primary forest (Site 5) and mixed disturbed forest and agricultural clearings (Site 6) on Catanduanes Island in 1988. The number of captures per net-night are given in parentheses. See text for site descriptions.

	Site 5	Site 6
<i>Cynopterus brachyotis</i>	5 (0.08)	33 (0.75)
<i>Eonycteris robusta</i>	0	2 (0.05)
<i>Eonycteris spelaea</i>	0	2 (0.05)
<i>Haplonycteris fischeri</i>	14 (0.21)	5 (0.11)
<i>Macroglossus minimus</i>	1 (0.15)	35 (0.78)
<i>Ptenochirus jagori</i>	0	19 (0.43)
<i>Pteropus leucopterus</i> *	0	2 (0.05)
<i>Rousettus amplexicaudatus</i>	0	1 (0.02)
Total fruit bats	20	99
Total net-nights	66	44
Fruit bats/net-night	0.30	2.25
Fruit bat species	3	8
Standardized total	20	97
Standardized bats/ net-night	0.30	2.20
Standardized species richness	3	7

* = Species excluded from standardized total to allow comparison to data from other islands.

marily in upland forest (Heaney et al. 1989), and rodents and shrews typically increase in diversity and abundance with increasing elevation (Rickart et al. 1991). It is almost certain that sampling of such habitats would add species to the current list.

Netting and trapping success.—We captured 119 fruit bats of eight species and seven insectivorous bats of six species in 110 net-nights at our forest sites in 1988. These samples for fruit bats are large enough for comparison with other sites in the Philippines. Standardized netting success (see methods) for fruit bats (Table 4) at the 1988 disturbed site (Site 6) was over seven times that in primary forest (Site 5; 0.3 vs. 2.2 bats per net-night); this difference is typical for disturbed vs. undisturbed sites on Negros and Leyte (Heaney et al. 1989). However, netting success was less than one-third that in comparable vegetation on Negros and Leyte. Proportionate composition of the fruit bat communities differed significantly

at the two sites (G-test, $G = 47.2$, $df = 7$, $P < 0.005$), with *Haplonycteris fischeri* most common in primary forest (Site 5) and *Cynopterus brachyotis*, *Macroglossus minimus*, and *Ptenochirus jagori* most common in disturbed habitat (Site 6). *Cynopterus brachyotis*, *Eonycteris spelaea*, *M. minimus*, and *Rousettus amplexicaudatus* typically are associated with moderately to heavily disturbed habitat in the Philippines, whereas *P. jagori* is a primary forest species that is most strongly associated with clearings in primary forest and lightly disturbed forest (Heaney et al. 1989, Heideman & Heaney 1989).

We captured 55 small mammals of three species in 1010 trap-nights during 1988. Trap success in primary forest (Site 5; 45 *Rattus everetti* and 1 *Rattus rattus* in 890 trap-nights) was 5.2/100 trap-nights, and in secondary forest (Site 6; 8 *R. everetti* and 1 *Rattus exulans* in 120 trap-nights) was 7.5/100 trap-nights; this is higher than in comparable habitat on Leyte or Negros by about a factor of 2. Species richness was quite low, which is typical of low elevation forest in the Philippines (Heaney et al. 1989, Rickart et al. 1991).

We captured eight species of insectivorous bats in caves and rock shelters (*Megaderma spasma*, *Emballonura alecto*, *Rhinolophus cf. arcuatus*, *R. inops*, *R. rufus*, *Hipposideros ater*, *Miniopterus australis*, and *M. schreibersii*) and observed one species of fruit bat (probably *Rousettus amplexicaudatus*; see species account). The cave fauna is generally similar to that found previously in Philippine caves (Taylor 1934, Lawrence 1939, Sanborn 1952), although no basis for quantitative comparison is available.

Biogeography.—Of the 35 species of mammals now recorded from Catanduanes, all but one are also known from neighboring Luzon. The one exception is *Saccolaimus saccolaimus*, a species that occurs from India to the Solomon Islands, and within the Philippines is known from Catanduanes, Mindanao, Mindoro, and Negros (Heaney

et al. 1987). The small number of specimens and their scattered occurrence suggest that this species is poorly sampled in the Philippines and might occur on Luzon. The presence of the remaining 34 species on Luzon is supportive of prediction 1 given above.

Only one species known from Catanduanes, *Phloeomys cumingi*, is restricted to Luzon and associated small islands. Approximately 18 additional murid rodents and one fruit bat are endemic to Luzon but are not known from Catanduanes. However, *Crocidura grayi* is restricted to Luzon and Mindoro, and preliminary studies by Heaney indicate that the mouse *Apomys microdon* may be restricted to Catanduanes and southern Luzon. Thus, although most of the mammalian fauna of Catanduanes is composed of widespread species, several species are specifically indicative of its past association with southern Luzon.

With 10 known species of non-volant mammals (eight of which are indigenous), Catanduanes clearly has a smaller fauna than Luzon, which has at least 35 (28 of which are indigenous; Heaney 1986). An island the size of Catanduanes in the Mindanao island group is expected to have about 12 indigenous species. Prediction 2 is thus supported only to the extent that the fauna is smaller than that of Luzon; it is also smaller than expected on the basis of islands in the Mindanao faunal region. Sampling of upland habitats is needed to determine the adequacy of current data.

Prediction 3 is supported by our findings: the nine species of fruit bats fall within the 95% confidence limits for other Philippine faunas (Heaney 1991). However, this is two species fewer than the predicted eleven species, and we suspect that other species (especially of *Pteropus*) remain to be discovered on Catanduanes.

Prediction 4 can be tested only partially with current data. Nearly all species known from Catanduanes are also found in lowland habitats on nearby Mt. Isarog on Luzon

(Rickart et al. 1991; specimens in USNM), and the upland rodents known from Mt. Isarog are absent; both observations support the prediction. However, some upland rodents might be present but currently unsampled, as noted above.

Comparison with birds.—The avifauna of Catanduanes is among the best-known of any on small islands in the Philippines (Gonzales 1983; Goodman & Gonzales 1989; Manuel 1937). The birds show biogeographic patterns that are strikingly similar to those of mammals. The avifauna of 146 species is entirely composed of species also found on Luzon, which has about 195 species (Hauge et al. 1986). With the exception of the endemic subspecies *Gallicolumba luzonica rubiventris*, a ground dove, all other reported subspecies on Catanduanes are also found on Luzon. The number of resident bird species in lowland forest and parang (anthropogenic grassland) on Catanduanes is 108, compared to 111 species in comparable habitat on Mt. Isarog, a relatively well-known mountain on the adjacent mainland of Luzon (Goodman and Gonzales 1990:33). However, of nine species (*Otus longicornis*, *Napothera rabori*, *Stachyris whiteheadi*, *Turdus poliocephalus*, *Brachypteryx montana*, *Ficedula hyperythra*, *Ficedula westermanni*, *Phylloscopus trivirgatus*, *Aethopyga pulcherrima*) associated with montane and mossy forest on Mt. Isarog, none are known from Catanduanes.

The avifauna thus conforms to the predictions presented above for the mammal fauna: it is shared entirely with Luzon, species richness is lower than that of Luzon, and it is composed of an attenuated portion of the fauna associated with lowland habitats on Luzon, with no obligate upland species. Because no analysis of species/area relationships has yet been carried out for birds in the Philippines, no quantification of this variable is possible. Nevertheless, the concordance of general patterns between these vertebrate groups is high. Further, more detailed comparisons are warranted.

Conclusion

Although still incompletely known, the mammal fauna of Catanduanes is clearly similar to that of adjacent Luzon, with no evidence of endemic species or representatives of other regions of the Philippines; in these ways it conforms to expectations for an island of its location and geological history. All predictions based on prior studies in the Philippines are supported, but the data are generally indicative of a smaller fauna than anticipated. Further field inventories of high elevation habitats are necessary to fully test predictions regarding the species richness and biogeographic origin of the fauna.

Acknowledgments

We thank A. Batal, R. Fernandez, S. M. Goodman, J. Ramos, D. A. Samson, and L. Tagat for energetic assistance with the field work, and L. Basmayor of Bicol State University for logistical assistance. The manuscript has benefited from editorial comments from M. D. Carleton, S. M. Goodman, P. D. Heideman, S. M. G. Hoffman, D. Klingener, and C. B. Robbins. We also thank L. Gordon and D. Schmidt for technical assistance. This research was supported by the National Science Foundation (BSR-8514223), the Smithsonian Institution Office of Fellowships and Grants, and the Philippine National Museum.

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